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EFFECTS OF FLUSHING NESTING GREATER PRAIRIE-CHICKENS IN ILLINOIS

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ABSTRACT.—Important reasons for evaluating researcher impact in nest studies include the possibility of increased abandonment, depredation, embryonic mortality, or bias of other parameters. From a 29-year data set of 1101 Greater Prairie-Chicken (*Tympanuchus cupido pinnatus*) nests in Illinois, we assessed the performance of 115 nests that were visited by investigators during egg laying or incubation. The minimum return rate for 107 hens flushed up to 5 times was 88% and apparently decreased ($G = 9.76$, df = 4, $P = 0.042$) with increased frequency of flushing caused by investigators. The success of 105 nests from which hens were flushed (68%) was higher ($G = 7.55$, df = 1, $P < 0.01$) than that of 840 undisturbed nests (53%) whose fates were determined prior to discovery. No desertions could be attributed to investigators activities. Embryonic mortality in disturbed nests appeared 3.7× higher ($Z = 4.59$, $P = 0.001$) than in undisturbed nests, but some egg removal by predators prior to our inspections may have biased results. Neither embryonic loss nor nest success was related to number of flushes during incubation. Nearly half of embryonic deaths that we could age in disturbed nests occurred before hen flushes, and most other losses, including whole clutches, were not clearly caused by investigator disturbance. *Received 30 June 1997, accepted 27 Oct. 1997.*

Information about researcher impact on nesting success is vital in studies of nesting birds (Götmark 1992). Precautions against negative impacts are especially important when studies involve endangered species, such as the Greater Prairie-chicken (*Tympanuchus cupido pinnatus*) in Illinois (Illinois Endangered Species Protection Act of 1972, amended 1977). Some investigations suggest researcher disturbance of nesting prairie-chickens might increase rates of abandonment (Davison 1940, Lehmann 1941, Yeatter 1943, Riley et al. 1992), depredation (Silvy 1968, Bowen 1971, Bowen et al. 1976), or egg breakage (Baker 1953). Other studies, however, report little or no impact with various nest-searching methods (Drobney 1973, Toepfer 1988), including cable-chain drags (Svedarsky 1983, 1988; J. R. Keir, pers. comm.). Search techniques in these studies also included use of dogs, rope drags, flushing bars, landowner interviews, observing departures and returns by nesting hens to morning and evening feeding sites, and most currently, radio telemetry. Thus, reasons for differences in researcher impact on clutch performance are not well known.

Events during two phases of Illinois' 29-year study (1963–1991) of 1101 Greater Prairie-Chicken nests suggested possible researcher-caused bias of egg success. During 1983–1987, egg success was no better in prairie-chicken nests from which parasitic Ring-necked Pheasant (*Phasianus colchicus*) eggs had been removed than for those from which pheasant eggs were not removed (Westemeier 1988). In 1990–1991, during efforts to increase genetic variability by exchanging eggs in two isolated remnant populations, embryonic mortality appeared exceptionally high, though seemingly unattributable to researcher activities (Westemeier et al. 1991). These findings prompted an expanded study.

Our objectives were to determine return rates of Greater Prairie-Chicken hens to their nests after investigator-induced disturbance, compare fates of investigator-disturbed with undisturbed nests, compare embryonic mortality between investigator-disturbed and undisturbed successful nests, and to determine if effects of investigator disturbance varied with stage in nesting cycle, or the number of hen flushes.

METHODS

Study areas and nest searching.—The study areas are located on the southern-till plain of Illinois near Bogota in Jasper County and near Kinmundy in Marion County (Fig.1). Flat-to-rolling prairies between wooded stream corridors characterized the region prior to European settlement. Both areas are now predominantly private farmlands of corn (*Zea mays*), soybeans

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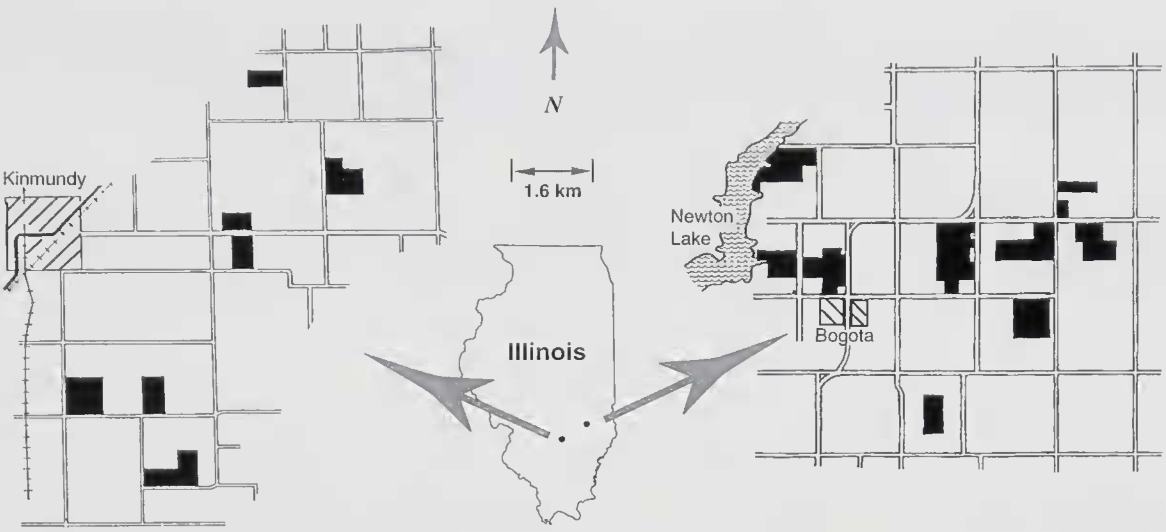

FIG. 1. Study areas near Bogota in Jasper County and near Kinmundy in Marion County, Illinois. Black blocks indicate sanctuary grasslands gradually established and annually managed for Greater Prairie-Chickens and associated wildlife during the study from 1963 through 1991.

(*Glycine max*), and wheat (*Triticum aestivum*). Fifteen scattered tracts (sanctuaries) ranging in size from 7–94 ha and totaling 551 ha (Fig. 1) were established by seeding cropland to grasses during the study (Sanderson et al. 1973; Westemeier 1973, 1988; Westemeier and Buhnerkempe 1983; Buhnerkempe et al. 1984; Westemeier et al. 1991).

During the first 22 years (1963–1984) of research, searching for nests on sanctuary grasslands did not begin until early June. A "hands-off policy" left most study nests undisturbed by researchers until hatching, depredation, abandonment, or other fate had terminated nesting efforts.

From 1985–1991, nest searching commenced by 1 May to allow removal of Ring-necked Pheasant eggs from active (i.e., first egg to termination) Greater Prairie-Chicken nests (Westemeier 1988). Earlier searching resulted in a higher proportion of total nests being found during egg laying or incubation (i.e., disturbed) than in previous years, but the change did not affect the relative stage of nesting (laying or incubating) at which active nests were found during the two periods.

Nest searches involved 2 or more persons walking abreast, each viewing a 1.5-m swath and using a 1.5-m staff to part vegetation at each possible nest site. Fields were searched once each year. We considered nest disturbance to include inspections of active nests even if hens were not flushed, because human scent and tracks were unavoidable. Active nests were marked with blaze orange ribbon placed 10 paces away on two sides of nests forming a right angle with each nest. Markers were tied to vegetation at heights of 30–35 cm. Nests that were already hatched or unsuccessful when found were tagged conspicuously at the immediate nest site for quick relocation and analysis.

Hen flushing.—Our first aim was to determine whether hens, if flushed, returned to their nests during the interval between flushing by investigators and nest termination. When hens were flushed from nests (most inadvertantly), search teams promptly left the sanctuary areas to allow for quick returns. The relatively few instances of intentional flushing for nest inspection were done when no rain was imminent, during midday (11:00–14:00), when temperatures were above 21° C, and at about weekly intervals. Hens were flushed once from 63% of the nests disturbed while active (n = 115) and more than once or not at all from the other 37%. Care was taken to minimize disturbance of vegetation surrounding nests, and attempts were made to restore disturbed plants to their original state.

Nest success.—Nests were considered successful if at least 1 Greater Prairie-Chicken egg hatched, but unsuccessful if only pheasant eggs (≥ 1) hatched in parasitized nests. Vance and Westemeier (1979) reported that parasitized prairie-chicken nests were less successful than unparasitized nests, but later data revealed no difference between unparasitized and parasitized nests (Westemeier 1988). Thus, parasitized nests were included in evaluating nest success.

We estimated nest success using apparent nest success since clutches found after termination (88%) or during incubation (9%) were not aged in this study. Mayfield's nest success (Mayfield 1975) was computed for a small sample (n = 27) of nests found during egg laying, which provided ages of those clutches. We assumed a laying rate of 1 egg/day. Klett and coworkers (1986) considered apparent nest success an appropriate estimator if successful and unsuccessful nests were found with equal probability, a condition that might be met in small units of habitat intensively searched for terminated nests, as in our situation. Nests destroyed by farming activities ($n \geq 92$) and nests of unknown fate (n = 56, $\bar{x}$ = 5.1%/year) were excluded from analyses of nest fate.

Embryonic mortality.—Intact eggs remaining in successful nests were opened and checked for germinal discs or embryos. Embryos were aged by criteria slightly modified from those for Ring-necked Pheasants (Labisky and Opsahl 1958) and Northern Bobwhites (*Colinus virginianus*; Roseberry and Klimstra

TABLE 1. Minimum returns by 107 Greater Prairie-Chicken hens to nests categorized according to flush frequency and stage of nesting when flushed by researchers, south-central Illinois, 1963–1991.

	Nesting stage when flushed							
	Incubating		Laying, incubating[a]		Unknown		Pooled	
Number of times flushed	Hens n	Returns[b] %	Hens n	Returns %	Hens n	Returns %	Hens n	Returns %
1	61	95.1	4	75.0	8	12.5	73	84.9
2	15	80.0	5	80.0			20	80.0
3	4	100.0	4	100.0			8	100.0
4	2	100.0	2	87.5			4	93.8
5					2	100.0	2	100.0
1–5	82	91.9	15	88.2	10	61.1	107	87.7

[a] Includes 6 hens flushed a total of 9 times during laying only; 9 hens were flushed during laying and incubation.
[b] Returns after flushing (minimum estimates) verified by subsequent nest success or by observing hens on nests prior to depredation or other fate.

1965). Both species incubate for about 23 days, compared with about 25 days for Greater Prairie-Chickens (Silvy 1968, McEwen et al. 1969, Svedarsky 1988). Rather than considering hatching success of total or fertile eggs, and to avoid bias from infertility or lack of incubation of fertile eggs, we directly evaluated the rate and timing of embryonic losses relative to disturbances. In assessing rates of embryonic mortality, prairie-chicken nests parasitized by pheasants were excluded because of possible bias associated with this interaction; excessive embryonic losses may be attributed to hens leaving their nests prematurely with parasitic broods prior to hatching of Greater Prairie-Chicken eggs (Vance and Westemeier 1979; Westemeier 1984, 1988; Westemeier and Edwards 1987).

Disturbed nests, those in which hens were laying or incubating when found, provided the best estimates of the numbers of total, fertile, and hatched eggs because of their fresh condition. Conversely, in undisturbed nests (eggs hatched, depredated, or abandoned upon discovery), egg shells or contents of intact eggs were often in poor condition by the time of discovery which resulted in minimum estimates of total eggs, fertile eggs, and hatched eggs. Consequently, we selected nests with egg shells and unhatched eggs still sufficiently fresh to detect germinal discs or embryos for calculating embryonic mortality. To verify success, we looked for distinct caps or pointed portions of eggs with detached membranes and pip lines characteristic of hatching. Dates of discovery for successful disturbed nests averaged 25 days earlier than successful undisturbed nests (8 June vs. 3 July, respectively). Thus, we hypothesized that the later dates might have allowed for a disproportionate removal of unhatched eggs by predators in undisturbed nests prior to our inspections. If so, such egg removal might have erroneously indicated less embryonic mortality in undisturbed nests than in disturbed nests.

Statistical analysis.—We used the log-likelihood ratio test (G-test) for contingency tables (Zar 1984) to determine if the frequency of hens returning to their nests (Table 1) was independent of (1) the number of times hens were flushed during incubation (data column one), (2) the number of times hens were flushed during incubation, laying, and unknown stages of nesting (pooled; data column four), and (3) flushing during incubation, or incubation and laying, regardless of the number of flushes (bottom row). Because of the unreliability of asymptotic P values with small sample sizes, we derived exact P values using permutation procedures (Agresti 1990).

We grouped data on nest fate into 3 sets similar to those of Evans and Wolfe (1967) for Ring-necked Pheasants because our methods were similar to theirs. Group I included nests from which hens were flushed at least once; Group II included a few nests found with hens on eggs but never flushed; and Group III included the majority of nests which were undisturbed because hatching, depredation, or other fate had occurred by the time they were found. G-test statistics for contingency tables were used to determine if nest success was independent of (1) flush frequency or (2) stage of nesting, and (3) whether it differed for nests involving hen flushing (Group I) and no disturbance (Group III). We also used G-tests for contingency tables to determine if frequency of nest abandonment or depredation differed between Group I and Group III. The effect of the number of human visits to each nest served as the predictor variable for a separate logistic regression (BMPD 1992) where nest success (score = 1) or failure (score = 0) was used as the dependent variable.

We compared the magnitude of embryonic mortality in disturbed and undisturbed nests using the Normal Approximation to the Mann-Whitney test (Zar 1984). For this test, the nest (% of embryos failing) was the unit of replication since embryos within a nest were not considered independent observations. We used a 1-way Kruskal-Wallis (K-W) test (BMPD 1992) to assess the association between the number of hen flushes and % embryonic mortality by grouping nests (1 flush, 2 flushes, ≥3 flushes).

RESULTS

Hen returns after flushing.—Of 1101 Greater Prairie-chicken nests found in south-central Illinois during 1963–1991, 115 were active (egg laying, n = 27; incubation, n = 78; unknown n = 10) upon discovery. Eight active nests had no hen flush; the other 107 hens flushed 1–5 times [$\bar{x}$ = 1.5 ± 0.9 (SD) flushes/hen]. After 163 flushes among 107 hens, we documented at least 143 returns (minimum rate = 88%) by hens to their nests prior to hatching, depredation, or abandonment. Small samples involving hens flushed 3–5 times appeared to show higher return rates than larger samples with hens flushed 1–2 times (Table 1). Statistically, however, the return rate decreased with increased frequency of hen flushing during incubation (G = 12.63, df = 3, $P < 0.01$) [e.g., we could not be certain that 6 of 15 incubating hens returned after two flushes (Table 1) because of depredation or abandonment after the second flush]. Similarly, minimum hen returns also showed a tendency to decline (G = 9.76, df= 4, P = 0.042) with increased frequency of flushing during incubation, laying, or unknown stages of nesting (pooled; Table 1). Again, we could not be certain that some hens returned, particularly after two flushes. Proportions of hens returning to nests during incubation, or both laying and incubation (two independent groups) did not differ (G_c = 1.32, df = 1, $P > 0.05$) regardless of flush frequency (Table 1).

Nest success after hen flushing.—Nest success did not differ whether hens were flushed 1, 2, or at least 3 times (G = 2.90, df= 2, $P > 0.05$); thus, nests experiencing at least 1 flush constituted Group I (Table 2). Within Group I, there was no difference in nest success between hens flushed during incubation and those flushed during laying (G_c = 1.58, df = 1, $P > 0.05$). Sample sizes in Group II were too small for tests. Success was actually higher (G_c = 7.55, df = 1, $P < 0.01$) for Group I (hens flushed by investigators) than for Group III (hens not flushed because hatching or other fate occurred prior to nest discovery). No relationship was shown between nest success and the number of times active nests (Groups I and II combined) were visited ($F_{1,111}$ = 0.46, $P > 0.05$). Successful, abandoned, and depredated nests were visited an average of 1.9, 2.0, and 2.1 times, respectively, prior to termination. Nest success calculated by the Mayfield exposure method was 59% for 27 nests found during the laying stage.

Abandonment and predation after hen flushing.—Frequency of abandonment was no higher for nests with hen flushes (Group I) than for undisturbed nests (Group III; G_c = 0.03, df = 1, $P > 0.05$; Table 2). Predation was less for nests from which hens were flushed (Group I) than for undisturbed nests (Group III; G_c = 9.04, df = 1, $P < 0.005$). In the few active nests where hens were not flushed (Group II), no abandonment was observed and depredation was 38%.

Embryonic mortality after hen flushing.—Of the 4,591 embryos in 479 successful Greater Prairie-Chicken nests from several counties in southcentral Illinois during the 29-year study, the rate of embryonic deaths

TABLE 2. Fate of 953 Greater Prairie-Chicken nests categorized according to degree of disturbance by nest searchers and stage of nesting, south-central Illinois, 1963–1991.

			Nest fate[a]					
			Successful		Abandoned		Depredated	
Category	Nesting stage when found	n	n	%	n	%	n	%
Group I (Hen flushed)	Incubating	81[b]	63	77.8	5	6.2	13	16.1
	Laying	14	8	57.1	1	7.1	5	35.7
	Unknown	10	0	0.0	0	0.0	10	100.0
	Total	105	71	67.6	6	5.7	28	26.7
Group II (Hen on, no flush)	Incubating	4	3	75.0	0	0.0	1	25.0
	Laying	4	2	50.0	0	0.0	2	50.0
	Total	8	5	62.5	0	0.0	3	37.5
Group III (No hen, undisturbed)	Hatched or unsuccessful							
	Total	840	446	53.1	40	4.8	354	42.1

[a] Omits nests of unknown fate and those destroyed by farming.
[b] Includes 7 nests found in laying stage with no hen present, but hens were later flushed during incubation.

(% in each nest) was 3.7× higher in disturbed nests [n = 56, $\bar{x}$ = 12.2 ± 2.2 (SE)], than in undisturbed nests (n = 423, $\bar{x}$ = 3.3 ± 0.4; Z = 4.59, P = 0.001). Embryonic mortality was unrelated to the number of flushes (1, 2, or ≥ 3) during incubation of successful unparasitized nests (K-W test: H = 0.38, df = 2, $P > 0.05$).

Clutch size was determined during incubation for 74 disturbed successful nests. These provided insight to possible bias in embryonic mortality resulting from egg predation during the 25-day average difference in discovery dates for disturbed and undisturbed nests. At our final post-hatch inspections, 1–3 intact eggs, or egg shells were missing in only 7 of the 74 nests of known clutch size. One egg disappeared between two inspections during incubation. Losses occurred in six other nests either during incubation or within 6 days after hatching. No losses of whole eggs or egg shells occurred in 67 nests; this included 16 nests that contained intact eggs when examined 7–14 days after hatching of other eggs.

Knowledge of hatch dates, inspection dates, and embryo age at death was sufficient in most disturbed nests with embryo losses to assess the timing of mortality relative to timing of hen flushes. Thus, 47% of the losses occurred prior to hen flushes, 20% coincided with hen flushing, 23% occurred well after hen flushes, and 10% occurred at an indeterminate time. Losses clearly resulting from nest searching included three eggs stepped on and one egg punctured, presumably by a hen's toenail when she flushed.

DISCUSSION

During this 29-year study, at least 88% of Greater Prairie-Chicken hens readily returned to their nests after 1–5 flushes. The calculated proportion of hens returning might have been considerably higher had we been able to verify some returns prior to depredations. As expected, disturbed nests, most of which were well along in incubation when found, were more successful than undisturbed nests already hatched or unsuccessful upon their discovery. Clutches found within a few days of hatching are more likely to hatch than those in the laying or early incubation stages because of the shorter interval between discovery and hatching (Mayfield 1975, Klett et al. 1986). This may partly account for the greater success of disturbed nests (68%) than undisturbed nests (53%). The 59% rate for Mayfield nest success also was relatively high (Jones 1988, McKee 1995) for 27 nests found during laying.

In our study, the probability of finding depredated prairie-chicken nests may have been at least equal to finding active nests. Incubating hens are often reluctant to flush (and be found), but bright, exposed, and often-scattered egg shells in depredated nests contrast with grassy vegetation. For these reasons, any bias may have favored our finding a greater proportion of unsuccessful nests rather than active and potentially more successful nests. This contention differs from that of Johnson (1994) for ducks. Thus, the relatively high success of disturbed prairie-chicken nests (68%) may have been even higher, not lower, than that for undisturbed nests that were no longer active when found.

For pheasant nests visited during incubation, Evans and Wolfe (1967) showed that rates of success and abandonment were not different from those of hens with which the investigator had no contact. Success for 934 prairie-chicken nests in 22 previous studies averaged 49% (Bergerud and Gratson 1988), which is similar to success of undisturbed nests in our study.

In our study, abandonment of 6 nests disturbed by researchers involved infertile eggs, possible pheasant interactions, or photographer disturbance (1 nest that also involved a non-researcher using a blind); none were clearly caused by investigator disturbance. Desertion of Prairie-Chicken nests (n = 876) averaged 7.3% in 18 previous studies (Bergerud and Gratson 1988). Other studies suggest that desertion may be increased if disturbance occurs during early stages of nesting for Greater Prairie-Chicken (Yeatter 1943), Blue Grouse (*Dendragapus obscurus*; Zwickel and Carveth 1978), and other species (Götmark 1992). Our limited observations indicated tolerance by hens flushed from eggs once the hens are at least midway through laying.

Nest predation following hen flushing was relatively low in this study (27%), possibly because of the short interval remaining before hatching in advanced clutches (Klett et al. 1986). Predation on 934 prairie-chicken nests in 22 previous studies averaged 39% (Bergerud and Gratson 1988), which is similar to predation on undisturbed nests (42%) in our study. When active nests were initially found by a crew of nest searchers, tracks and human scent were uniformly distributed over the searched portions of fields, and 63% of 115 nests were visited only once. Thus, there were no direct trails, which are commonly thought to lead predators to nests, to nearly two-thirds of the disturbed nests. In an extensive review, Götmark (1992) found no or little evidence for increased predation by mammals on bird nests as a result of investigator disturbance. In Kansas, Bowen et al. (1976) found no difference in depredation rates on dummy nests walked to daily compared with unvisited control nests. However, normal feeding patterns of Greater Prairie-Chickens tending real nests were disrupted in an earlier study (Bowen 1971). Flushing incubating prairie-chickens from their nests during midday (as in our study) is likely to be additive to their normal absence for feeding during early morning and late afternoon (Silvy 1968, Bowen 1971, Svedarsky 1979).

For average clutches of 11.2 fertile eggs, a 12.2% embryonic mortality rate means 1.4 dead embryos per disturbed active nest if losses prior to hen flushes (nearly half in our study) are included, compared with a normal loss of 0.4 embryo per undisturbed clutch. Other studies indicate embryonic mortality (unsuccessful fertile eggs/total fertile eggs) well below 10% (Gross 1930, Hamerstrom 1939, Yeatter 1943, Svedarsky 1988, Jones 1988), and even no loss (Schwartz 1945, Baker 1953, Silvy 1968, Drobney 1973). However, removal of unhatched eggs by predators prior to post-hatch inspections may have biased data from other studies, as in our study.

By 7 days post hatch, sterile eggs or those with dead embryos may be sufficiently putrid to be unappealing to predators. Our experience suggests that partial disappearance of eggs or egg shells mostly occurs between late incubation and 1 week post hatch. Since we typically delayed final nest inspections to about 4 days post hatch, bias associated with nest discovery dates seems minimal because much of the time frame for egg loss may have applied to disturbed and undisturbed nests alike. Yet, despite precautions taken to minimize negative effects to disturbed clutches in Illinois, embryonic mortality appeared excessive. Some hens may be slow in returning to their clutches after being flushed, and the eggs may subsequently experience excess exposure to sun, cooling, or drying with attendent weakening and killing of embryos.

We conclude that our nest study methods have allowed a minimum of 88% return of disturbed hens to their nests and nest success at least as good as their undisturbed counterparts. However, embryonic mortality in disturbed nests appeared high even with considerations for bias. The causes of embryonic mortality remain largely enigmatic and perhaps exclusive to Illinois. A loss of egg quality possibly stemming from genetic deficiencies should not be ignored because Greater Prairie-Chicken populations in Illinois are small, isolated, and had declined alarmingly during the period (1987–1991) of highest embryonic loss (Westemeier et al. 1991). In future studies, flushing of nesting hens should be minimal, but when flushing is necessary, the time of day, date, weather conditions, and egg exposure should be routinely recorded for evaluations of embryonic mortality. Improved knowledge of laying times and daily off-nest feeding periods by incubating hens would facilitate nest inspection and obviate hen flushing. An aging guide for Greater Prairie-Chicken embryos is needed. Controlled experiments on the effects of various stresses on survival of Greater Prairie-Chicken embryos and pen studies on interactions with pheasants might provide needed information.

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